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Comparison of Several Biological Markers used for Stock Identification of Sockeye Salmon *(Oncorhynchus nerka)* in Northern British Columbia and Southeast Alaska

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COMPARISON OF SEVERAL BIOLOGICAL MARKERS USED FOR STOCK IDENTIFICATION OF SOCKEYE SALMON (Oncorhynchus nerka) IN NORTHERN BRITISH COLUMBIA AND SOUTHEAST ALASKA.

by

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ABSTRACT

Wood, C. C., G. T. Oliver, and D. T. Rutherford. 1988. Comparison of several biological markers used for stock identification of sockeye salmon (Oncorhynchus nerka) in northern British Columbia and Southeast Alaska. Can. Tech. Rep. Fish. Aquat. Sci. 1624: 44 p.

Fisheries agencies in Canada and the USA are engaged in cooperative research on stock identification of sockeye salmon (Oncorhynchus nerka) under the auspices of the Pacific Salmon Commission. To date this research has focussed on the use of four types of "biological markers" - scale patterns, age composition, parasite prevalence and biochemical genetic data. In this report, we describe how these markers have been used and compare their utility with respect to (1) potential for stock differentiation, (2) stability over time, (3) homogeneity within populations and (4) ease of sampling. Selected data are summarized from unpublished reports of the Pacific Salmon Commission and files of participating agencies to substantiate these comparisons.

RÉSUMÉ

Wood, C. C., G. T. Oliver, and D. T. Rutherford. 1988. Comparison of several biological markers used for stock identification of sockeye salmon (Oncorhynchus nerka) in northern British Columbia and Southeast Alaska. Can. Tech. Rep. Fish. Aquat. Sci. 1624: 44 p.

Les organismes qui s'occupent des pêches au Canada et aux E.-U. participent sous les auspices de la Commission du saumon du Pacifique à des recherches conjointes sur l'identification des stocks de saumon rouge (Oncorhynchus nerka). Jusqu'ici, ces recherches ont été axées sur l'utilisation de quatre types de "marqueurs biologiques": les structures d'écaille, la composition par âge, la fréquence des parasites et les données génétiques biochimiques. Dans ce rapport, nous décrivons de quelle façon on a utilisé ces marqueurs et nous comparons leur utilité pour ce qui est de 1) la possibilité de différencier les stocks, 2) de la stabilité avec le temps, 3) de l'homogénéité au sein des populations et de 4) la facilité de l'échantillonnage. Nous faisons un résumé de données choisies tirées de rapports non publiés de la Commission du saumon du Pacifique et de dossiers d'organismes participants pour étayer ces comparaisons.

INTRODUCTION

Recent advances in statistical methods and computational capabilities have made it easier to estimate the stock composition of mixed-stock fishery samples by examining biological attributes that differ between stocks (e.g. Milner et al. 1981, 1983; Fournier et al. 1984; Pella and Milner 1987; Millar 1987; Wood et al. 1987a). Where satisfactory "biological markers" can be found, stock composition can be determined routinely without resorting to expensive and laborious tagging studies. A variety of biological markers have been studied in sockeye salmon populations, and the reliability of stock composition estimates using these markers is potentially equal to that of estimates derived from tagging studies.

The purpose of this report is to describe and compare the various kinds of biological markers which have proven useful for differentiating sockeye salmon (Oncorhynchus nerka) populations in northern British Columbia and Southeast Alaska. In particular, we evaluate four types of biological markers -- scale patterns, freshwater age, prevalence of the brain parasite Myxobolus neurobius, and biochemical genetic differences -- with respect to (1) potential for stock differentiation, (2) stability over time, (3) homogeneity within populations and (4) ease of sample collection.

METHODS

DATA SOURCES

Cooperative research between Canada and the United States on stock identification procedures for Pacific Salmon (genus Oncorhynchus) was first initiated under the International Salmon Tagging Program in 1982. Following ratification of the Pacific Salmon Treaty in 1985, further cooperative research has been encouraged under the auspices of the Pacific Salmon Commission. Over the past five years, researchers with the Alaska Department of Fish and Game (ADFG), the Canada Department of Fisheries and Oceans (CDFO), the National Marine Fisheries Service (NMFS), and the Pacific Salmon Commission (PSC) have collected extensive data on characteristics of sockeye salmon populations in British Columbia and Southeast Alaska. Although few of these data have been published, they are available from unpublished reports to the Pacific Salmon Commission and from unpublished files of the four agencies involved.

Most of the data presented in this report have been taken from an unpublished report prepared by the Joint Northern Boundary and Transboundary River technical committees entitled "Stock Identification of Sockeye Salmon

Using Biological Markers" which is available as Report TCNB/TR (87) 1 from the Pacific Salmon Commission, 1155 Robson St., Suite 600, Vancouver, B.C. V6E 1B9. We also cite the work of individual investigators and agencies as appropriate in the text.

SAMPLE COLLECTION AND ANALYSIS

The procedures for sample collection, scale analysis, parasite examination, and electrophoretic analysis used by CDFO staff are the same as those described in Wood et al. (1987c). ADFG and NMFS staff used similar procedures although details of collection and analysis vary among agencies. In general, investigators attempted to obtain random samples that were representative of the stocks sampled. Sample size targets ranged from 50-100 fish for the brain parasite examinations, to 100-150 fish for electrophoretic analysis, to as high as 2100 fish for scale data in populations with several important age groups.

The scale pattern data presented in this report pertain only to age 1.3 (5 year old) sockeye since this is the principal age class in northern British Columbia and Southeast Alaska. Scale pattern data are summarized for three growth zones: zone 1 refers to growth during the first year in fresh water; zone 2, to "plus" growth during the second year in fresh water prior to entering the sea; and zone 3, to growth occurring at sea during the remainder of the second year (Fig. 1). The number of circuli (NC) and the incremental distances or width (ID) between circuli were recorded for each growth zone along the anterior-posterior axis from projected images at 100X magnification. Incremental distances were measured between inside edges of circuli.

Electrophoretic variation was typically assayed at 23 to 25 loci using horizontal starch gel electrophoresis as described by Utter et al. (1984). Only data from up to five polymorphic loci (PGM-1, PGM-2, LDH-4, IDH-3, IDH-4) available for most populations are considered in this report (Table 1). The most common allele was designated type 100 following the procedures of Allendorf and Utter (1979).

Similarity dendrograms were constructed to demonstrate the relative degree of differentiation that is potentially available using various biological markers. These dendrograms were based on a distance index proposed by Wood et al. (1987a) which is similar to Nei's genetic distance (Nei 1972); they were constructed using the single linkage method (Pielou 1977) to highlight potential misclassifications.

DESCRIPTION OF BIOLOGICAL MARKERS

SCALE PATTERNS

The pattern of circulus formation in sockeye scales records an individual fish's growth history (e.g. Burgner 1964; Ward and Larkin 1964, Bugaev 1987). Most of the scale features used to differentiate stocks are associated with growth in fresh water where different stocks occupy discrete environments that may differ in temperature and in the availability of food (e.g. Henry 1961). Scale patterns are particularly useful for sockeye salmon because the vast majority of juvenile sockeye inhabit lakes for a year or more, so that members of a population probably share a fairly uniform environment, at least in comparison with river-rearing salmonids. A large number of scale features can be measured from a single scale (e.g. Marshall et al. 1987) but usually these can be expressed as two or three uncorrelated markers using principal components analysis. The number of circuli (NC), and the width (ID) for each year of freshwater growth are the statistics most commonly used to summarize scale pattern data.

Scale patterns have proven very useful for in-season management within large river systems (e.g. the Fraser River, Cook and Guthrie 1987) or where a relatively small number of stocks contribute to mixed-stock fisheries (e.g. the Lynn Canal, McPherson 1986). Their utility for analyzing mixed-stock fishery samples with contributions from a large number of stocks ("coastwide mixtures") is less certain owing to variation in scale patterns from year to year and age group to age group which necessitates extensive resampling of individual stocks (see next section). A total of about 120 stocks have been sampled by staff of the ADFG, CDFO, and the PSC but only about 60 are resampled routinely each year (Appendix 1). ADFG staff use scale pattern data to estimate stock composition for principal age classes of sockeye caught in various marine fisheries in southeast Alaska in-season on a weekly basis. The PSC also analyses scales from fisheries in north and central British Columbia and Southeast Alaska to identify Fraser River sockeye in catches. At present, CDFO does not use scale pattern analysis (alone) to estimate contributions of non-Fraser River sockeye stocks in marine fisheries.

AGE COMPOSITION

Sockeye salmon populations frequently differ dramatically in both freshwater and marine age composition (Foerster 1968). Freshwater age typically varies from 0. (no freshwater annular marks indicating that fry did not spend a winter in fresh water) to 3. (three winters spent in fresh water). Age 1. sockeye are prevalent in most coastal and clearwater interior lake systems whereas 2. sockeye are prevalent in glacial lakes (Wood et al. 1987c).

Marine age is a useful marker, in principle, since much variation exists among populations. However, its practical value is limited owing to great variability from year to year within a stock and because sockeye of different age groups often migrate through fisheries at different times during a season (e.g. McPherson 1986). Even so, age composition can be used for estimating stock composition where samples can be obtained over the entire run, and pooled to provide representative "seasonal" samples of the catch. The age composition in a seasonal mixture sample of fish from a particular stock should then be representative of that stock; otherwise the age composition of fish from that stock sampled in the fishery in any single week may not be representative. The PSC uses total age along with scale parameters and length to assess maximum contributions in northern areas by Fraser River sockeye stocks since the vast majority of fish from this watershed are age 1.2 (J. C. Woodey, PSC, 1155 Robson St., Suite 600 Vancouver, B.C., V6E 1B9, pers. comm.).

PARASITE PREVALENCE

Parasite prevalence refers to the proportion of fish in a population that are infected by a particular parasite. Many different parasites are found in sockeye salmon, but for stock identification in the northern British Columbia - Southeast Alaska area, research has focussed on a protozoan brain parasite (Myxobolus neurobius). Little is known of the life cycle of this species but the presence of this parasite is thought to be determined by characteristics of the freshwater rearing environment. Again, because sockeye juveniles share the same lake environment, they probably share the same risk of being parasitized. A total of about 80 sockeye populations in British Columbia and Southeast Alaska have been examined for this parasite by CDFO (L. Margolis and C. C. Wood, Pacific Biological Station, Nanaimo, B.C., unpubl. data) and NMFS (J. H. Helle and D. A. Moles, Auke Bay Laboratory Auke Bay, Alaska, pers. comm.) (Appendix 2). The majority of Southeast Alaskan stocks have a high prevalence of infection whereas relatively few Canadian stocks are infected. For this reason, the proportion of parasitized sockeye in some mixed-stock fisheries can be interpreted as the maximum contribution from Southeast Alaskan stocks. Of course, this interpretation may be misleading for those fisheries exploiting significant numbers of unparasitized Alaskan stocks. Brain parasite data have been used to estimate stock composition in weekly sockeye samples from various marine fisheries in Southeast Alaska and northern British Columbia, and in test fisheries in the Stikine, Taku and Nass rivers.

Other parasites have been used to differentiate up to seven stocks in the Fraser River system with excellent precision (Bailey and Margolis 1987). However, the prevalence of these parasites is less well studied and their usefulness in the Northern Boundary area has not been demonstrated.

BIOCHEMICAL GENETIC MARKERS

Methods for detecting genetic differences among stocks are gaining widespread popularity in fisheries research. Several different procedures for detecting genetic variation have been developed. The most widely used involves electrophoresis to detect variation in the electrical properties of simple enzymes. The genetic mechanism for this variation then must be determined in cross-breeding studies. At least 60 sockeye populations in British Columbia and Southeast Alaska (Fig. 1 and Appendix 3) have been screened for differences in the frequency of alternative alleles at approximately 25 loci (Utter et al. 1984; Wood et al. 1987b; Quinn et al. 1987; J. Helle, Auke Bay Laboratory, Auke Bay, Alaska, pers. comm.; B. E. Riddell and C. C. Wood, Pacific Biological Station Nanaimo, B.C., unpubl. data). In sockeye, only about six of these enzymes are polymorphic (i.e. exhibit more than one allele), but four of these vary greatly among populations and are very useful for stock identification.

COMPARISON OF BIOLOGICAL MARKERS

POTENTIAL FOR STOCK DIFFERENTIATION

Some biological markers permit differentiation of more stocks than others. For example, within individual fish the brain parasite, Myxobolus neurobius, is either present or absent (two states), and thus, is useful for differentiating only two stocks. No unique stock composition estimates can be found for mixture problems where the number of stocks being resolved exceeds the number of observable states available (e.g. Pella and Milner 1987). Similarly, sockeye can be one of four possible freshwater ages -- 0., 1., 2., or 3. These age groups occur in varying proportions among stocks making age composition data of greater but still very limited value in differentiating stocks. In principle, scale patterns can differentiate many more groups because there are measured differences and conceivably infinite variations in scale features among stocks. However, in practice, only a limited range of values occur which leads to overlap in the frequency distributions of scale features from stock to stock, thereby limiting the number of stocks that can be differentiated. Electrophoretic methods typically detect two to six different genotypes at each locus in sockeye populations and again each fish is one of only several types. However, when two different loci are considered simultaneously, each with, say three genotypes, the potential number of categories increases to 3^2 or nine. Thus, using markers in combination dramatically increases the stock resolution potential for stock differentiation (e.g. Wood et al. 1987b, 1988).

Similarity among stocks can be defined in terms of a "distance" calculated from the probabilities of drawing a fish with particular scale patterns, (or genotypes) from each population (see Methods). The similarity dendrograms illustrated in Figures 3-6 show which sockeye populations resemble

one another in terms of three basic scale features (Fig. 3), freshwater age (Fig. 4), brain parasite prevalence (Fig. 5) and five polymorphic enzymes (combined, Fig. 6). The distance metric is identical in Figures 3-6 to permit comparison. The vertical lines linking horizontal lines indicate the relative distance separating the linked stock-group; stocks joined by vertical lines on the extreme left hand margin are virtually indistinguishable using the marker in question whereas those joined together farther to the right are easier to differentiate. Although the dendrogram based on three scale features (Fig. 3) shows the greatest potential for stock differentiation, it should be noted that the distance measurement in the dendrogram reflects both real differences among stocks and differences due to sampling error associated with small samples. Markers which can take on many different values (such as scale circulus counts) will be most affected by sampling errors so that large sample sizes are required to detect real differences among stocks where differences in scale features are not large. Consequently, it is unclear whether the actual differences among stocks (as opposed to the observed samples) are truly as useful as suggested by the dendrogram in Figure 3.

STABILITY OF MARKERS OVER TIME

Another important criterion for selecting biological markers is whether the marker is stable over time. A marker is stable if the probability of occurrence of the various states of that marker (e.g. of an allele or age group) does not change from year to year within a population. Stability is a desirable property since it implies that individual stocks need not be resampled frequently.

Scale patterns are expected to vary from year to year within populations because they reflect growth history which probably depends on climate, fish density and the availability of food. This is evident to some extent in Table 2 which summarizes available data from sockeye populations that have been sampled at least twice within the last 20 years. In general, however, variation within stocks seems to be less than variation among stocks. Simulation studies are required to determine the degree to which stock composition estimates are influenced by this kind of variability. Although superior estimates are usually obtained using scale data from the corresponding year (Marshall et al. 1984), it may still prove useful to use scale data from preceding years (i.e. "historical" data) when current data are unavailable. This is an important topic for further research since the cost effectiveness of scale analysis will be greatly determined by the amount of annual resampling that is required.

Freshwater age composition also varies from year to year in some populations (Table 2) but again, where variation within populations is less than between populations, it may be possible to get satisfactory stock composition estimates with historical data. Marine age composition often varies dramatically from year to year (Foerster 1968).

The prevalence of the brain parasite Myxobolus neurobius appears to be remarkably stable from year to year (Table 3) although the mechanism for this stability is not understood. The best evidence for stability comes from Great Central and Sproat Lakes on Vancouver Island where the parasite prevalence has varied narrowly between 0 - 8.4% and 99.4 - 100.0%, respectively, over a period of 8 years (Quinn et al. 1987).

The theory of population genetics predicts that all genetic markers will be stable within isolated randomly mating populations provided there is no survival advantage associated with the alternative genes. Indeed, virtually all sockeye stocks that have been sampled repeatedly exhibit very little variation in allele frequencies (Table 3). It is this property that makes genetic markers attractive for stock identification studies. The data in Tables 2 and 3 span only several years at most. Thus, any gradual trends in population characteristics would not be detected. Even where markers appear to be stable over several years, it would be prudent to resample populations at regular intervals (perhaps every few generations) to be confident of long term stability.

HOMOGENEITY OF MARKERS WITH RESPECT TO AGE AND SEX

Another desirable property of biological markers is that their probability of occurrence within a population be independent of age or sex. For example, it has been demonstrated that scale features typically vary from age group to age group within a population (Anas and Murai 1969). This complicates the stock composition analysis and necessitates much larger sample sizes to ensure adequate sampling of all principal age groups. Freshwater and early marine scale features do not appear to be influenced by the sex of the fish (Table 4).

Marine age composition often varies greatly between the sexes: for example, fish maturing after only one year at sea are almost invariably male ("jacks") (e.g. Foerster 1968). Freshwater age composition does not appear to vary with sex (Table 4).

Brain parasite prevalence and genetic markers are not dependent on sex (Table 5). There is some indication, however, that brain parasite prevalence is slightly lower in sockeye that spend less than one year in fresh water (Wood et al. 1987c) presumably because they are exposed to the parasite source for a shorter time. This is unlikely to be of consequence since age 0. fish are rare in most populations.

SAMPLING CONSIDERATIONS

Scales are collected routinely from most major commercial fisheries and spawning escapements of sockeye salmon to determine age composition. Scales can be collected without difficulty from commercial catches when the fish are delivered to processing facilities since handling, damage to the

fish, and interference with processing routines is minimal. Scale samples can also be collected from spawning escapements without harming fish. However, because environmental conditions change from year to year and the distribution of scale traits is complicated, large sample sizes and independent analyses for all major age classes are required. Trained personnel are also required for consistent interpretation of scale features. Duplicate scale impressions are made on acetate cards; these are compact and can be exchanged or stored for future reference.

Age composition data are collected routinely from most fisheries and spawning populations for other stock assessment objectives. Resorption of scales in spawning escapement and some catch samples can make determination of marine age difficult, but otoliths, fin rays, or length frequency curves can be used to corroborate ages. Freshwater age composition can usually be determined even from badly resorbed scales (K. Rutherford, Pacific Biological Station, Nanaimo, B.C., V9R 5K6, pers. comm.).

Brain parasite samples (whole heads) can usually be collected in processing plants but care must be taken to obtain complete and uncontaminated samples. The parasite Myxobolus neurobius forms spores which will not deteriorate until the brain rots so that escapement samples can be collected from carcasses. Of course, if carcasses are unavailable it is necessary to kill fish to obtain the brain samples. Large sample sizes are not necessary due to the simple statistical distribution of the trait (i.e. presence or absence). Samples can be preserved by freezing.

Tissues required for electrophoresis are often more difficult to obtain from processors because the eye, liver and heart tissues may be removed from the fish at slightly different locations during processing making it difficult to cross-reference samples. Furthermore, the removal of muscle tissue usually reduces the market value of fish and makes samples more expensive to obtain. For this reason, enzymes found only in muscle tissue have seldom been used to estimate the stock composition of commercial sockeye fisheries. Samples must be frozen immediately and stored at very low temperatures to preserve enzyme activity; some loss of enzyme activity has been encountered during long fishery openings when fish have been dead for up to four days before sampling. Escapement samples must be obtained from live fish. Preservation of tissue samples can be difficult in remote field locations since dry ice or adequate freezer space is usually unavailable locally and the duration of sampling activities is limited by the length of time samples can be kept. These problems can be avoided by preserving samples in liquid nitrogen, although this is a more expensive procedure. Intermediate sample sizes (approximately 100) are required to determine allele frequencies with acceptable precision for most applications. Enzyme activity cannot be perserved indefinitely except in supercold freezers at -80°C but photographic records of electrograms can be maintained.

DISCUSSION

Recent research coordinated by the Pacific Salmon Commission has led to the development of sophisticated stock identification techniques for sockeye salmon using biological markers (e.g. scale data, Marshall et. al. 1984, 1987; parasite and genetic data, Wood et. al. 1987 a, b). Using these techniques concurrently, it is possible in principle (as shown using simulated mixtures), to detect contributions by up to 40 or 50 individual sockeye stocks (Wood et al. 1988). The feasibility of this method for solving practical problems depends to a large extent on the availability of representative data to characterize the major spawning populations.

Scale pattern data generally show excellent potential for differentiating sockeye populations. However, variation in scale patterns within populations from year to year and among age groups may necessitate annual collection of large samples from individual populations. In many situations this requirement will preclude the use of scale pattern data for stock composition analysis in-season, before spawning samples have been collected. Moreover, the collection of large, annual samples of scales from many (often remote) spawning populations will not always be feasible. Thus, analyses using scale pattern data are probably most applicable to mixed-fishery problems involving relatively few, easily sampled stocks. Alternatively, it may be possible to rely on samples obtained in previous years for particular stocks where between-year variation in scale patterns is small in comparision to the differences that exist between these and other stocks. Simulation studies would be required to evaluate the utility of using samples from previous years in different applications, but judging from the data presented in this report, the opportunities for using historical data do not seem promising for problems involving many stocks.

Another approach to simplifying the problems associated with scale pattern data that has been adopted by ADFG involves collecting a single sample representing a composite of stocks to reduce the overall number of escapement samples required. For example, all stocks returning to the Nass River can be represented by a single Nass River composite sample collected from a test fishery in the lower river over the entire migration period. For this procedure to be reliable, it is essential that either: (1) all stocks contributing to the composite sample have very similar scale pattern characteristics as compared to samples from other drainages; or (2) that the contributing stocks are represented in the composite sample in proportion to their relative abundance in the mixed-stock fishery being examined. Stock composition estimates will be biased if neither of these conditions is fulfilled (Wood et al. 1987a). Although it should be possible to obtain composite samples containing correctly weighted proportions of contributing stocks from test fisheries within major river systems, it is more difficult to ensure that the relative proportions of contributing stocks observed within a river do not vary among fishing locations that may be hundreds of kilometers distant. Nevertheless, this procedure may still prove expedient for routine management objectives where trends in relative estimates of stock composition can be more important than absolute estimates of stock composition.

The potential for using biochemical genetic marks for stock identification of Pacific salmon is very promising. There is growing evidence to support expectations from genetic theory that allele frequencies at polymorphic loci are very stable from year to year in Pacific salmon populations. Unfortunately, relatively few polymorhic loci have been identified in sockeye salmon populations, so that the potential for differentiating sockeye populations using naturally-occurring biochemical genetic marks is rather limited at present. The prevalence of the brain parasite Myxobolus neurobius also appears to be very stable over time, and when used in conjunction with allele frequency data at known polymorphic loci, permits differentiation of up to about ten stock-groupings with acceptable accuracy and precision (Wood et al. 1987a). The stability properties of these genetic and parasite markers implies that samples need not be collected from spawning populations annually and that in-season estimation of stock composition is possible. Hopefully, with further research, additional polymorphic loci or suitable parasites can be identified to increase the number of sockeye stocks or stock groupings that can be differentiated reliably.

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Table 1. Enzymes and tissues used to investigate genetic variation in sockeye salmon at five commonly used loci. Buffers used were (AC) an amine citrate buffer described by Clayton and Tretiak (1972), and (RW) a Tris, citric acid, lithium hydroxide, and boric acid buffer described by Ridgway et al. (1970).

Enzyme	Tissue	Locus	Buffer
Isocitrate dehydrogenase	Liver	IDH-3,4	AC
Lactate dehydrogenase	Liver	LDH-4	RW
Phosphoglucomutase	Heart	PGM-1	AC
	Liver	PGM-2	AC

Table 2. Year to year variability in biological markers from scales. Scale features pertain only to age 1.3 fish.

Stock	Year	Sample size		Scale feature[1]						Fresh water age composition				Sample size
				NC1	NC2	NC3	ID1	ID2	ID3	0	1	2	3	
Tahltan L.[2]	1982	139	mean	14.14	3.14	26.78	34.83	5.44	86.93	0.00	0.82	0.18	0.00	441
			SD	1.96	1.12	2.68	5.05	1.80	9.83					
	1983	111	mean	12.46	2.10	35.35	35.35	5.08	95.76	0.00	0.94	0.06	0.00	1,883
			SD	0.18	0.09	0.21	1.63	0.90	3.30					
	1984	44	mean	11.27	1.36	27.50	31.33	2.28	97.39	0.00	0.93	0.07	0.00	85
			SD	1.23	0.53	2.72	3.27	1.02	9.70					
	1985	26	mean	11.42	1.31	25.31	31.52	2.69	97.46	0.00	0.98	0.02	0.00	126
			SD	1.72	0.47	2.02	4.08	1.27	6.58					
	1986	200	mean	11.84	1.53	27.39	31.56	2.74	94.28	0.00	0.90	0.10	0.00	719
			SD	0.11	0.04	0.18	1.07	0.38	2.56					
Chutine L.[2]	1984	15	mean	7.80	1.53	30.67	23.74	2.90	111.24	0.00	0.57	0.42	0.01	80
			SD	1.78	0.92	3.60	4.69	2.07	11.97					
	1985	7	mean	7.29	3.71	28.57	21.55	8.19	108.02	0.00	0.44	0.55	0.00	45
			SD	2.36	2.14	3.31	5.87	5.09	10.00					
	1986									0.00	0.41	0.59	0.00	61
Chutine R.[2]	1984	36	mean	8.36	2.03	28.58	25.28	4.27	107.16	0.02	0.95	0.03	0.00	61
			SD	2.34	1.63	3.71	7.23	3.79	13.00					
	1985	16	mean	8.00	2.31	29.06	23.27	5.44	111.03	0.04	0.96	0.00	0.00	47
			SD	2.03	1.01	2.46	6.02	2.65	9.43					
	1986									0.01	0.94	0.05	0.00	99
Scud R.[2]	1984	18	mean	8.17	2.39	30.06	25.58	5.06	109.63	0.23	0.73	0.05	0.00	44
			SD	1.65	0.98	2.98	4.64	2.52	10.03					
	1985	39	mean	8.77	1.85	28.64	26.81	4.15	109.95	0.21	0.79	0.00	0.00	66
			SD	2.01	0.90	2.43	6.50	2.21	8.79					

Table 2 (cont'd)

Stock	Year	Sample size		Scale feature[1] NC1	NC2	NC3	ID1	ID2	ID3	Fresh water age composition 0	1	2	3	Sample size
Iskut R.[2]	1983									0.00	1.00	0.00	0.00	51
	1984	70	mean	8.73	2.36	28.58	24.05	5.01	113.45	0.02	0.95	0.02	0.00	140
			SD	1.70	1.18	3.71	4.24	2.95	14.08					
	1985	152	mean	8.79	1.94	29.48	25.95	4.24	113.59	0.18	0.78	0.05	0.00	156
			SD	1.72	0.92	2.67	5.53	2.26	9.54					
	1986									0.00	0.97	0.03	0.00	68
Babine L.[3]	1967	506	mean	11.11	-----	29.79	32.63	-----	113.45					
			SD	2.01	-----	3.12	5.80	-----	14.08					
	1968	1172	mean	12.42	-----	28.56	37.94	-----	109.18					
			SD	1.82	-----	3.15	5.78	-----	11.21					
	1982									0.00	1.00	0.00	0.00	158
Hugh Smith L.[4]	1982	50	mean	11.20	2.02	32.30	26.94	4.06	108.71	0.00	0.93	0.07	0.00	3,009
			SD	1.70	0.82	2.20	3.56	1.52	8.64					
	1983	10	mean	8.90	1.70	33.30	25.10	3.84	122.48	0.00	0.67	0.32	0.00	1,107
			SD	0.55	0.26	0.76	4.89	3.01	8.69					
	1984									0.00	0.70	0.30	0.00	1,591
	1985	10	mean	11.30	1.90	28.50	28.47	3.66	105.74	0.00	0.75	0.25	0.01	1,170
			SD	1.50	0.99	1.18	14.00	9.29	29.32					
	1986	100	mean	11.51	2.79	30.54	29.43	5.80	105.61	0.00	0.94	0.06	0.00	666
			SD	0.79	0.51	0.88	7.48	4.66	12.08					
McDonald L.[4]	1982	50	mean	8.20	0.88	33.20	19.05	1.78	116.08	0.00	0.79	0.21	0.00	629
			SD	1.60	0.44	2.70	3.56	1.02	9.65					
	1983	10	mean	9.70	1.30	30.60	24.00	2.08	116.38	0.00	0.55	0.45	0.00	1,366
			SD	0.52	0.21	0.83	5.95	2.27	13.44					
	1984	10	mean	7.89	1.00	33.70	21.23	1.42	114.35	0.00	0.83	0.17	0.00	929
			SD	0.78	0.00	2.63	2.52	0.79	11.19					

Table 2 (cont'd)

Stock	Year	Sample size		Scale feature[1] NC1	NC2	NC3	ID1	ID2	ID3	Fresh water age composition 0	1	2	3	Sample size
McDonald L.[4]	1985	10	mean	8.40	2.30	32.20	18.57	4.75	116.10	0.00	0.77	0.23	0.00	537
			SD	1.71	1.06	1.55	19.85	8.72	18.81					
	1986	100	mean	8.58	1.90	32.30	23.08	4.17	111.28	0.00	0.71	0.29	0.00	497
			SD	0.58	0.57	2.54	4.51	8.82	49.31					
Naha L.[4]	1982	50	mean	11.10	0.50	31.00	27.69	1.02	106.43	0.00	0.98	0.02	0.00	184
			SD	1.70	0.61	2.00	3.81	1.27	9.65					
	1983	10	mean	13.30	1.40	33.90	31.42	2.59	120.45	0.00	0.85	0.15	0.00	1,648
			SD	0.40	0.22	1.02	4.49	2.04	14.09					
	1984	5	mean	13.40	1.00	30.20	33.12	0.30	114.86	0.00	0.84	0.16	0.00	500
			SD	1.34	0.00	1.30	3.35	0.68	7.48					
	1985	10	mean	13.60	2.00	28.20	33.63	3.71	109.68	0.00	1.00	0.00	0.00	405
			SD	2.37	0.67	4.76	15.09	5.17	57.03					
	1986	10	mean	13.80	2.20	32.80	33.10	4.11	121.16	0.00	0.90	0.10	0.00	810
			SD	1.62	1.14	1.99	14.71	9.71	40.62					
Helm L.[4]	1982	50	mean	13.90	3.32	30.20	33.27	7.11	113.03	0.00	1.00	0.00	0.00	276
			SD	1.80	0.96	2.50	4.32	2.29	13.46					
	1983	11	mean	12.27	2.18	30.82	31.66	4.62	122.17	0.00	0.24	0.76	0.00	274
			SD	0.62	0.18	0.54	5.53	1.87	14.24					
	1984									0.00	0.69	0.31	0.00	29
	1985	10	mean	12.50	3.80	29.70	31.17	7.21	439.20	0.00	0.98	0.02	0.00	367
			SD	2.17	1.14	2.31	13.60	8.78	38.56					
	1986	10	mean	13.00	3.20	30.10	31.29	5.89	109.14	0.00	0.97	0.03	0.00	320
			SD	0.94	0.63	2.85	11.15	3.91	48.59					
Johnson L.[4]	1982	50	mean	12.30	2.26	31.60	29.97	4.83	115.57	0.00	0.65	0.35	0.00	337
			SD	2.10	0.83	2.30	4.57	2.03	9.14					
	1983	10	mean	13.80	1.10	33.00	34.95	1.68	121.08	0.00	0.59	0.41	0.00	563
			SD	0.29	0.10	0.98	3.98	1.53	14.75					
	1984	10	mean	13.50	1.00	30.80	32.56	0.23	118.16	0.00	0.38	0.62	0.00	240
			SD	2.59	0.00	2.25	5.81	0.72	6.84					

Table 2 (cont'd)

Stock	Year	Sample size		Scale feature[1]						Fresh water age composition				Sample size
				NC1	NC2	NC3	ID1	ID2	ID3	0	1	2	3	
Johnson L.[4]	1985	10	mean	12.60	2.60	30.40	31.60	5.11	111.38	0.00	0.50	0.49	0.01	358
			SD	2.95	1.17	2.87	33.51	9.47	44.40					
	1986	3	mean	13.00	2.67	33.67	35.64	6.27	131.49	0.00	0.60	0.40	0.00	10
			SD	1.00	1.16	1.53	10.02	7.64	15.04					
Kegan L.[4]	1982	50	mean	11.50	0.82	33.20	27.43	1.78	117.60	0.00	0.78	0.22	0.00	1,776
			SD	1.20	0.60	2.40	2.79	1.27	10.41					
	1983	10	mean	9.90	1.10	35.30	1.05	2.08	126.70	0.00	0.59	0.41	0.00	1,699
			SD	0.61	0.10	0.75	4.13	0.93	8.50					
	1984	10	mean	10.30	1.10	34.90	24.18	0.94	116.05	0.00	0.59	0.41	0.00	321
			SD	1.64	0.32	3.30	4.15	1.29	6.97					
	1985	10	mean	10.80	1.70	33.60	26.82	3.66	130.58	0.00	0.79	0.21	0.00	444
			SD	1.40	0.82	2.68	14.64	8.49	36.74					
	1986	10	mean	10.50	1.10	34.30	26.85	1.91	126.24	0.00	0.88	0.12	0.00	208
			SD	1.08	0.32	2.11	11.92	3.14	47.81					
Klakas L.[4]	1982	50	mean	7.70	3.74	31.20	18.29	7.37	113.03	0.00	0.98	0.02	0.00	356
			SD	1.70	1.31	3.60	2.79	2.54	13.46					
	1983	10	mean	9.00	1.20	32.70	23.09	2.62	123.32	0.00	0.89	0.11	0.00	691
			SD	0.47	0.13	0.68	4.43	0.83	17.03					
	1984	10	mean	7.80	1.10	30.80	15.04	0.94	108.94	0.00	0.96	0.04	0.00	270
			SD	0.44	0.10	0.79	3.14	1.00	12.79					
	1985	10	mean	7.00	1.60	32.80	15.06	2.90	130.45	0.02	0.95	0.03	0.00	318
			SD	1.41	0.70	2.62	15.99	6.38	46.88					
W. Chuck L.[4]	1982	50	mean	14.90	0.82	29.70	39.62	1.78	109.22	0.00	0.85	0.15	0.00	332
			SD	2.00	0.56	3.20	5.08	1.27	12.19					
	1983	10	mean	13.80	1.00	31.40	38.74	1.80	118.19	0.00	0.84	0.16	0.00	1,755
			SD	0.29	0.00	0.73	4.22	0.89	12.99					
	1984	9	mean	12.89	1.00	29.67	33.95	1.13	111.73	0.00	0.75	0.15	0.00	572
			SD	1.62	0.00	2.92	4.16	1.09	12.37					

Table 2 (cont'd)

Stock	Year	Sample size		Scale feature[1]						Fresh water age composition				Sample size
				NC1	NC2	NC3	ID1	ID2	ID3	0	1	2	3	
W. Chuck L.[4]	1985	10	mean	14.10	1.70	30.20	37.82	3.20	127.00	0.00	0.82	0.18	0.00	686
			SD	2.33	0.48	1.88	19.21	6.35	25.84					
	1986	10	mean	12.80	1.50	32.00	34.47	2.97	116.74	0.00	0.93	0.07	0.00	359
			SD	1.32	0.71	2.50	16.49	5.70	31.97					
Luck L.[4]	1982	50	mean	12.00	1.04	32.10	28.45	2.03	117.09	0.00	0.86	0.14	0.00	365
			SD	1.40	0.49	2.60	3.05	1.02	10.67					
	1983	10	mean	11.20	1.00	33.50	28.78	0.97	126.95	0.00	0.82	0.18	0.00	445
			SD	0.68	0.00	0.48	3.49	1.59	10.50					
	1984	10	mean	11.80	1.00	32.10	29.29	1.52	114.27	0.00	0.85	0.15	0.00	335
			SD	1.23	0.00	2.47	2.24	0.83	11.30					
	1985	10	mean	11.20	2.30	30.50	27.94	5.03	120.14	0.00	0.76	0.24	0.00	265
			SD	1.88	1.83	3.84	11.25	14.20	48.00					
	1986	10	mean	9.90	3.70	33.70	22.86	7.70	123.39	0.00	0.67	0.33	0.00	222
			SD	1.37	1.16	2.83	1.37	9.95	36.49					
Salmon Bay L.[4]	1982	50	mean	10.80	1.02	33.80	23.88	2.03	111.76	0.00	0.91	0.09	0.00	1,302
			SD	1.80	0.25	2.70	3.81	0.51	8.13					
	1983	10	mean	11.00	1.80	31.80	26.31	3.51	111.05	0.00	0.85	0.15	0.00	527
			SD	0.49	0.25	0.83	4.41	0.69	11.68					
	1984	10	mean	11.80	1.40	31.30	28.19	2.49	113.03	0.00	0.99	0.01	0.00	592
			SD	1.40	0.90	2.36	3.94	1.83	11.08					
	1985	10	mean	10.50	2.30	31.30	23.47	5.23	117.98	0.00	0.89	0.11	0.00	1,342
			SD	1.84	1.06	2.60	11.21	12.24	39.88					
	1986	10	mean	10.70	3.10	33.50	23.85	6.27	114.30	0.00	0.87	0.13	0.00	1,257
			SD	2.41	0.99	3.03	18.21	8.54	39.42					
Red Bay L.[4]	1982	50	mean	14.40	0.44	30.30	35.05	0.76	105.16	0.00	0.91	0.09	0.00	316
			SD	1.60	0.64	1.90	3.80	1.02	9.40					
	1983	10	mean	9.10	1.00	31.40	23.90	1.04	106.86	0.00	0.62	0.38	0.00	367
			SD	0.28	0.00	1.04	3.14	1.38	10.53					
	1984	10	mean	9.10	1.50	30.10	20.93	1.96	95.63	0.00	0.90	0.10	0.00	271
			SD	0.53	0.22	1.16	5.61	2.27	21.83					

Table 2 (cont'd)

Stock	Year	Sample size		Scale feature[1] NC1	NC2	NC3	ID1	ID2	ID3	Fresh water age composition 0	1	2	3	Sample size
Red Bay L.[4]	1985	10	mean	11.80	1.20	26.40	29.44	1.98	105.54	0.00	0.85	0.15	0.00	520
			SD	1.93	0.63	3.81	14.75	4.49	43.90					
	1986	10	mean	10.70	1.50	30.50	28.93	2.74	106.17	0.00	0.92	0.08	0.00	498
			SD	1.57	0.71	2.76	12.25	6.34	40.82					
Thoms L.[4]	1982	50	mean	14.50	0.42	28.40	37.34	0.76	107.44	0.00	0.47	0.53	0.00	508
			SD	1.90	0.54	7.60	3.81	1.02	19.55					
	1983	10	mean	13.50	1.30	28.90	34.11	2.26	109.50	0.00	0.29	0.71	0.00	419
			SD	0.45	0.15	0.85	4.62	2.33	10.71					
	1984	10	mean	13.40	1.00	30.20	34.26	1.68	110.49	0.00	0.56	0.44	0.00	607
			SD	0.43	0.00	0.96	6.63	1.24	16.79					
	1985	10	mean	13.00	1.70	27.00	36.30	3.43	110.16	0.00	0.52	0.48	0.00	337
			SD	0.86	0.30	0.56	7.33	2.49	8.62					
	1986	4	mean	13.25	1.75	29.25	35.94	3.43	117.22	0.00	0.11	0.87	0.02	375
			SD	0.95	0.25	1.44	9.61	0.50	18.28					

[1]NC1=number of circuli in first freshwater zone.
NC2=number of circuli in plus growth zone.
NC3=number of circuli in first ocean zone.
ID1=width of first freshwater zone (in mm at 100X magnification)
ID2=width of plus growth zone
ID3=width of first ocean zone
[2]From Wood et al. (1987c)
[3]Unpubl. data, C. C. Wood, Pacific Biological Station, Nanaimo, B.C., V9R 5K6
[4]Unpubl. data, G. T. Oliver, ADFG, P.O. Box 3-2000, Juneau, AK 99802

Table 3. Year to year variability in brain parasite prevalence and common (100) allele frequencies for three of the most polymorphic loci.

		Brain parasite		Frequency of common alleles for polymorphic enzymes					
Stock	Year	Sample size	Proportion infected	Sample size	PGM-1 freq.	Sample size	PGM-2 freq.	Sample size	LDH-4 freq.
Tahltan L.[1]	1982	30	0.000	96	0.188	98	0.959	98	0.378
	1983	100	0.000	89	0.140	102	0.936	102	0.431
	1985	99	0.010	98	0.189	97	0.969	100	0.430
Chutine L.[1]	1984	100	0.090	99	0.328	99	0.854	100	0.945
	1985	50	0.040	49	0.357	49	0.837	50	0.950
	1986	64	0.016						
Chutine R.[1]	1984	62	0.470	61	0.246	61	0.820	62	0.855
	1985	50	0.440	48	0.167	48	0.792	50	0.880
	1986	50	0.400						
Scud R.[1]	1984	50	0.660	48	0.188	48	0.833	50	0.890
	1985	67	0.490	65	0.162	65	0.831	68	0.926
Iskut R.[1]	1983	110	0.150	60	0.183	111	0.784	112	0.915
	1984	151	0.150	149	0.164	148	0.824	151	0.854
	1985	336	0.140	335	0.204	331	0.796	332	0.886
Babine R.[2]	1982	60	0.000	448	0.184	475	0.732	481	0.961
	1983	200	0.000	197	0.188	249	0.755	251	0.977
Meziadin L.[2]	1982			92	0.174	99	0.955	99	0.434
	1983	130	0.000	94	0.117	96	0.953	100	0.325
	1984	100	0.000	100	0.110	100	0.935	100	0.430
	1986	299	0.000	289	0.087	293	0.961	287	0.401
Fred Wright[2] L.	1983	130	0.020	98	0.107	99	0.838	100	0.690
	1984	100	0.060	99	0.091	99	0.843	96	0.589
	1986	189	0.005	190	0.145	182	0.827	190	0.750
Bowser L.[2]	1983	130	0.010	46	0.087	65	0.923	65	0.762
	1984	87	0.000	86	0.145	85	0.912	86	0.791
	1986	100	0.000	99	0.101	99	0.955	100	0.755
Damdochax[2] L.	1983	130	0.860	73	0.151	100	0.860	100	0.860
	1984	100	1.000	98	0.138	98	0.857	99	0.818
	1986	100	0.910	100	0.150	99	0.850	100	0.860

Table 3 (cont'd)

Stock	Year	Brain parasite		Frequency of common alleles for polymorphic enzymes					
		Sample size	Proportion infected	Sample size	PGM-1 freq.	Sample size	PGM-2 freq.	Sample size	LDH-4 freq.
Long L.[2]	1983	100	0.000	83	0.470	84	0.845	84	0.994
	1984	154	0.000	100	0.540	100	0.815	98	0.980
Owikeno[2]	1982	150	1.000	100	0.270	99	0.833	100	0.960
L.	1984	100	0.990	100	0.280	99	0.879	100	0.980
Hugh Smith[3]	1982	30	0.933	50	0.190	50	0.850	50	0.910
L.	1983	75	0.947	96	0.172	95	0.879	96	0.979
McDonald L.[3]	1982	30	0.933	50	0.080	50	0.850	50	0.980
weir	1983	25	0.880	93	0.124	99	0.849	100	0.960
McDonald L.[3]	1983	75	0.947	100	0.129	100	0.848	100	0.965
	1986	50	0.980						
Naha R.[3]	1983	57	0.298	104	0.125	104	0.745	104	0.923
	1984	100	0.390	104	0.152	104	0.640	100	0.840
	1986	79	0.481						
Helm L.[3]	1983	50	1.000	50	0.120	50	0.760	50	0.960
	1986	50	1.000	39	0.051	39	0.731	40	0.963
Kegan L.[3]	1982	30	1.000	100	0.360	99	0.551	100	0.995
	1983	50	0.880	100	0.335	100	0.540	100	1.000
	1986	50	1.000						
Karta L.[3]	1982	30	0.967	50	0.200	50	0.760	50	0.950
	1983	50	0.940	100	0.175	100	0.715	100	0.995
	1986	10	0.800						
Luck L.[3]	1983	50	0.980	50	0.110	50	0.790	50	0.950
				36	0.139	37	0.689	40	0.913
Salmon Bay[3]	1982	30	1.000	69	0.232	69	0.841	69	0.993
L.	1983	45	0.889	75	0.227	75	0.883	76	0.993
	1986	41	0.976						
Red Bay L.[3]	1983	70	1.000	69	0.159	57	0.430	68	0.949
	1986	53	0.962	40	0.237	39	0.577	40	0.975

Table 3 (cont'd)

Stock	Year	Brain parasite		Frequency of common alleles for polymorphic enzymes					
		Sample size	Proportion infected	Sample size	PGM-1 freq.	Sample size	PGM-2 freq.	Sample size	LDH-4 freq.
Thoms L.[3]	1983	75	0.987	74	0.339	75	0.640	75	1.000
	1986	50	1.000						
Speel L.[3]	1983	50	0.900	100	0.180	100	0.820	100	0.950
	1986	100	0.850						

[1]From Wood et al. (1987c)
[2]Unpubl. data, C. C. Wood and B. E. Riddell, Pacific Biological Station, Nanaimo, B.C., V9R 5K6
[3]Unpubl. parasite data, D. A. Moles, Auke Bay Laboratory, Auke Bay, AK 99821
Genetic data from Utter et al. (1984) and Winans and Helle (1988)

Table 4. Variability with respect to sex of biological markers from scales. Scale features pertain only to age 1.3 fish.

Stock	Year	Sex	Sample size		Scale feature[1]						Freshwater age			Sample size
					NC1	NC2	NC3	ID1	ID2	ID3	0.	1.	2.	
Iskut R.[2]	1985	M	34	mean	8.76	1.88	29.79	25.55	4.02	112.90	0.17	0.79	0.04	66
				SD	1.50	0.98	2.82	5.22	2.56	10.20				
		F	93	mean	8.81	1.96	29.48	26.08	4.20	113.78	0.21	0.74	0.05	84
				SD	1.84	0.87	2.56	5.88	2.05	9.67				
Little Tatsamenie[3] L.	1985	M	21	mean	8.52	1.71	26.76	27.24	4.25	100.20	0.02	0.57	0.40	54
				SD	2.48	1.01	2.47	6.16	2.84	11.90				
		F	12	mean	9.00	1.42	27.00	30.65	2.97	105.50	0.00	0.57	0.40	44
				SD	2.37	0.79	1.81	7.12	1.93	11.90				
McDonald L.[4]	1982	M	29	mean	8.59	1.07	34.07	19.08	1.95	117.65	0.00	0.74	0.26	335
				SD	1.52	0.26	2.46	3.86	1.06	8.33				
		F	21	mean	8.19	1.00	32.00	18.97	1.66	113.77	0.00	0.84	0.16	294
				SD	1.66	0.00	3.66	3.48	0.93	11.23				
Naha L.[4]	1982	M	21	mean	11.90	1.10	30.48	29.41	1.59	106.93	0.00	1.00	0.00	97
				SD	1.84	0.45	2.16	4.27	1.43	10.03				
		F	29	mean	10.69	1.00	31.48	26.64	0.52	107.09	0.00	0.97	0.03	87
				SD	1.42	0.00	1.84	2.97	0.81	10.03				

[1]NC1=number of circuli in first freshwater zone.
NC2=number of circuli in plus growth zone.
NC3=number of circuli in first ocean zone.
ID1=width of first freshwater zone (in mm at 100X magnification).
ID2=width of plus growth zone.
ID3=width of first ocean zone.
[2]From Wood et al. (1987c)
[3]Unpubl. data, C. C. Wood, Pacific Biological Station, Nanaimo, B.C., V9R 5K6
[4]Unpubl. data, G. T. Oliver, ADFG, P.O. Box 3-2000, Juneau, AK 99802

Table 5. Variability with respect to sex of brain parasite prevalence and common (100) allele frequencies for three of the most polymorphic loci.

				Brain parasite		Frequency of common alleles for polymorphic enzymes					
Stock	Year	Sex	Age	Sample size	Proportion infected	Sample size	PGM-1 freq.	Sample size	PGM-2 freq.	Sample size	LDH-4 freq.
Iskut R.[1]	1985	M	1.3	50	0.16	50	0.240	50	0.750	50	0.890
			All	96	0.20	96	0.214	96	0.771	96	0.885
		F	1.3	132	0.17	132	0.235	132	0.803	133	0.891
			All	177	0.15	177	0.209	177	0.814	177	0.890
Little Tatsamenie[1] L.	1985	M	1.3	27	0.00	27	0.185	27	0.926	27	0.833
			All	55	0.00	55	0.100	55	0.927	55	0.873
		F	1.3	14	0.00	14	0.143	14	0.964	14	0.821
			All	44	0.00	43	0.151	43	0.884	44	0.909
Owikeno L.[1]	1984	M	1.2	47	0.98	47	0.245	47	0.883	47	0.989
			All	61	0.98	61	0.246	60	0.900	61	0.984
		F	1.2	19	1.00	19	0.237	19	0.868	19	1.000
			All	39	1.00	39	0.346	39	0.846	39	0.974
Meziadin L.[1]	1984	M	2.2	29	0.00	29	0.241	29	0.948	29	0.466
			All	48	0.00	47	0.277	47	0.936	47	0.426
		F	2.2	36	0.00	36	0.222	36	0.917	36	0.389
			All	51	0.00	52	0.192	52	0.933	52	0.423

[1]Unpublished data, C. C. Wood, Pacific Biological Station, Nanaimo, B.C., V9R 5K6

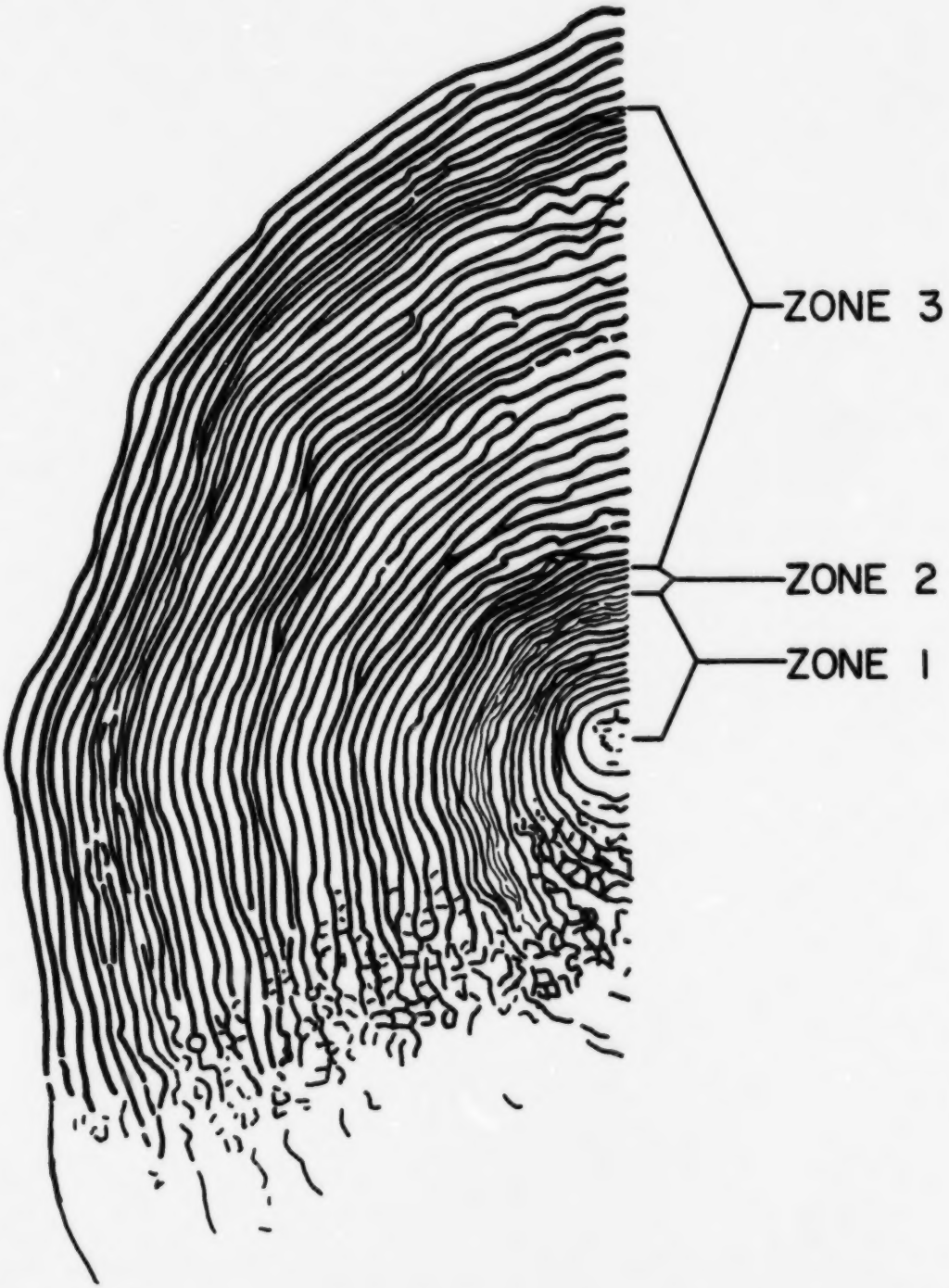

Fig. 1. Diagram of typical sockeye salmon scale explaining growth zone definitions for age 1.2 fish.

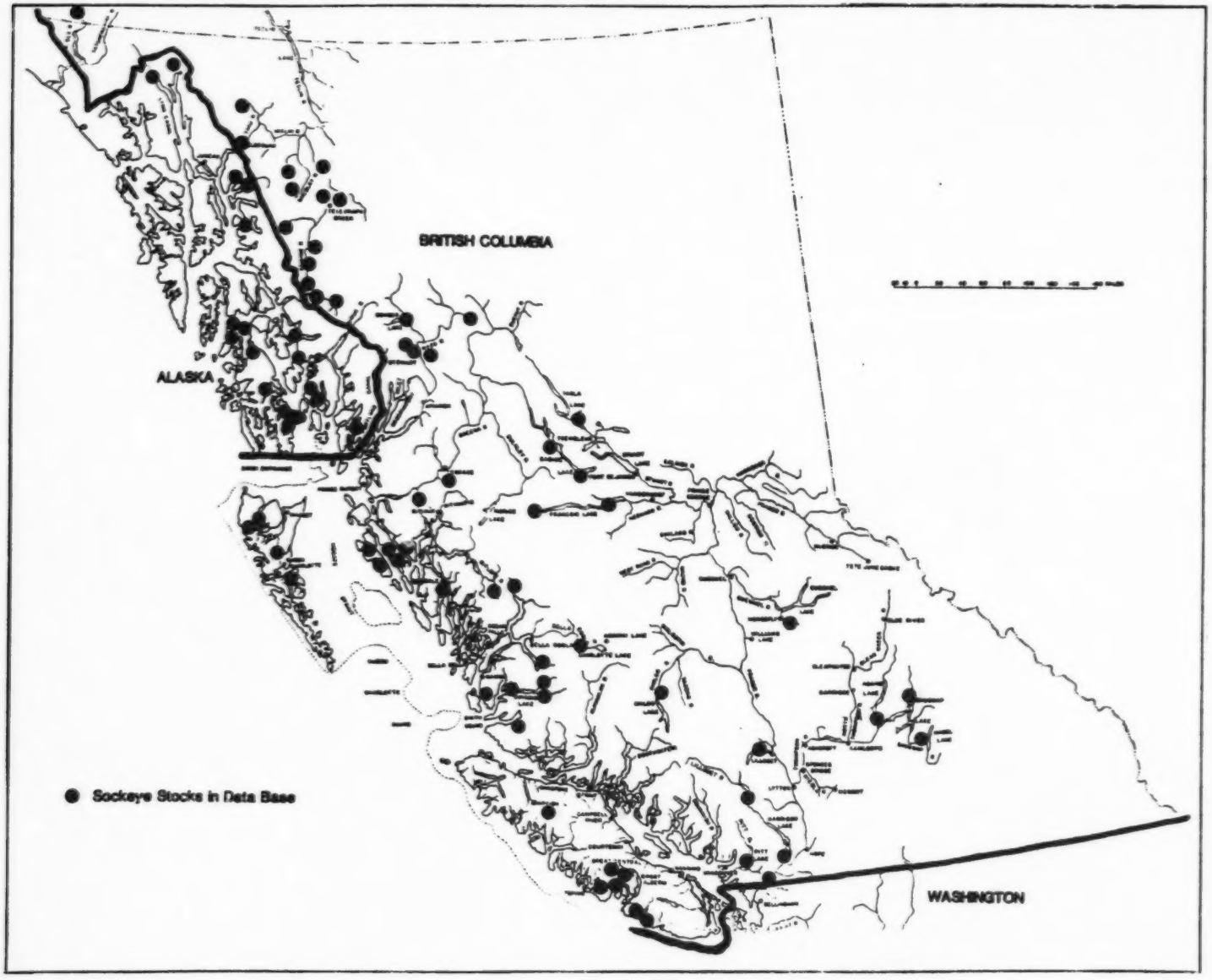

Fig. 2. Sockeye salmon populations in southeast Alaska and northern British Columbia for which matched brain parasite, electrophoretic, age composition and scale pattern data are available.

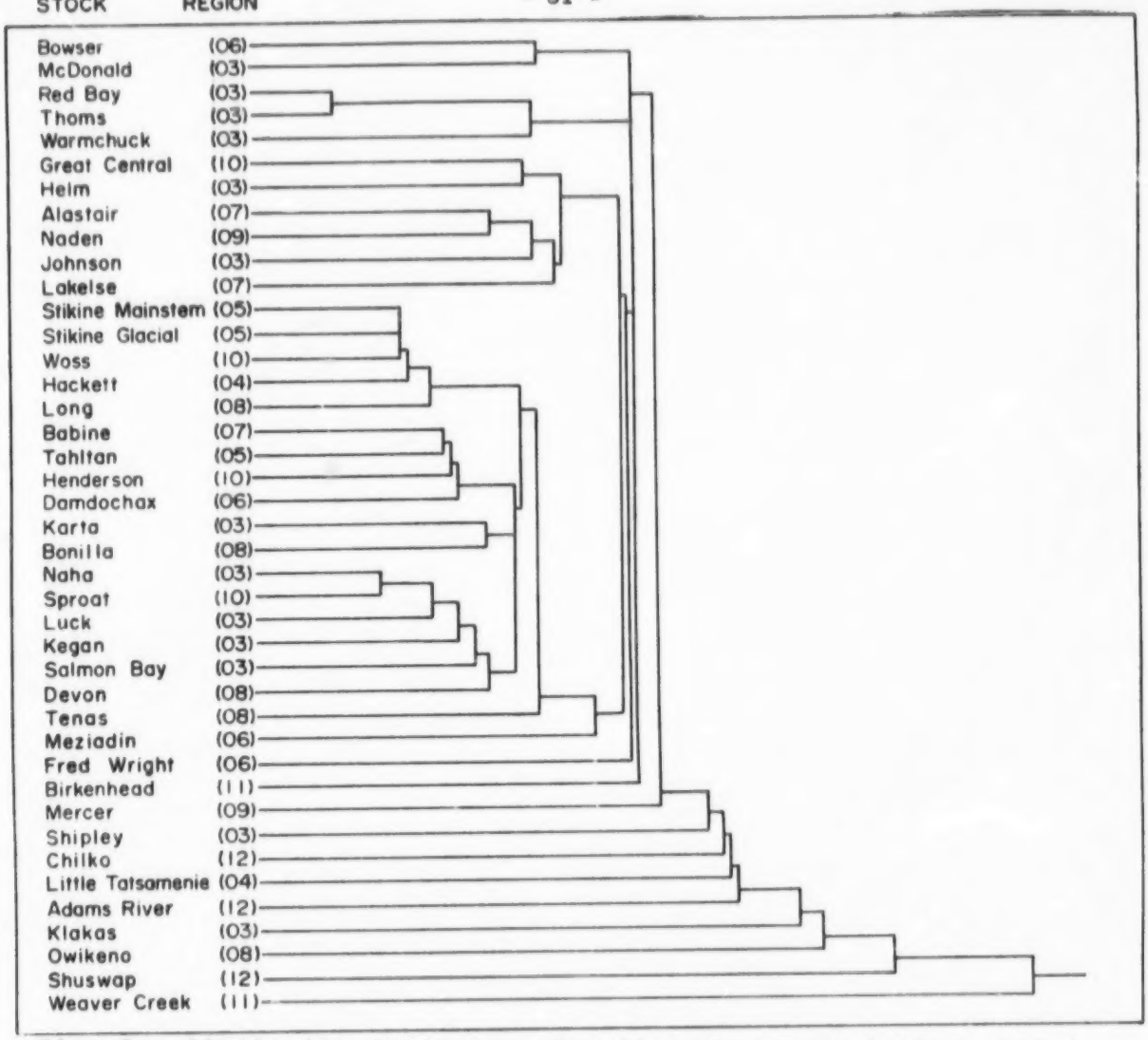

Fig. 3. Similarity dendrogram for 41 sockeye populations based on scale pattern data only. Three scale features were considered for age 1.3 sockeye only - the number of circuli laid down during (1) the first year of freshwater growth, (2) during "spring growth" in fresh water in the second year, and (3) during marine growth in the remainder of the second year. Samples range in size from 4 to 125 (10 samples < 15) and were collected between 1979 and 1986. Distances between populations calculated using procedure of Wood et al. (1987a) for Figures 3-6. Regions are defined in Figures 3-6 as: Alsek watershed (01): Lynn Canal Southeast Alaska District 112 (02): Southest Alaska Districts 101-111 (03): Taku watershed (04): Stikine watershed (05): Nass watershed (06): Skeena watershed (07): British Columbia central and north coast Areas 5-12 (08): Queen Charlotte Islands (09): Vancouver Island (10): lower Fraser watershed (11): upper Fraser watershed, above Hell's Gate (12).

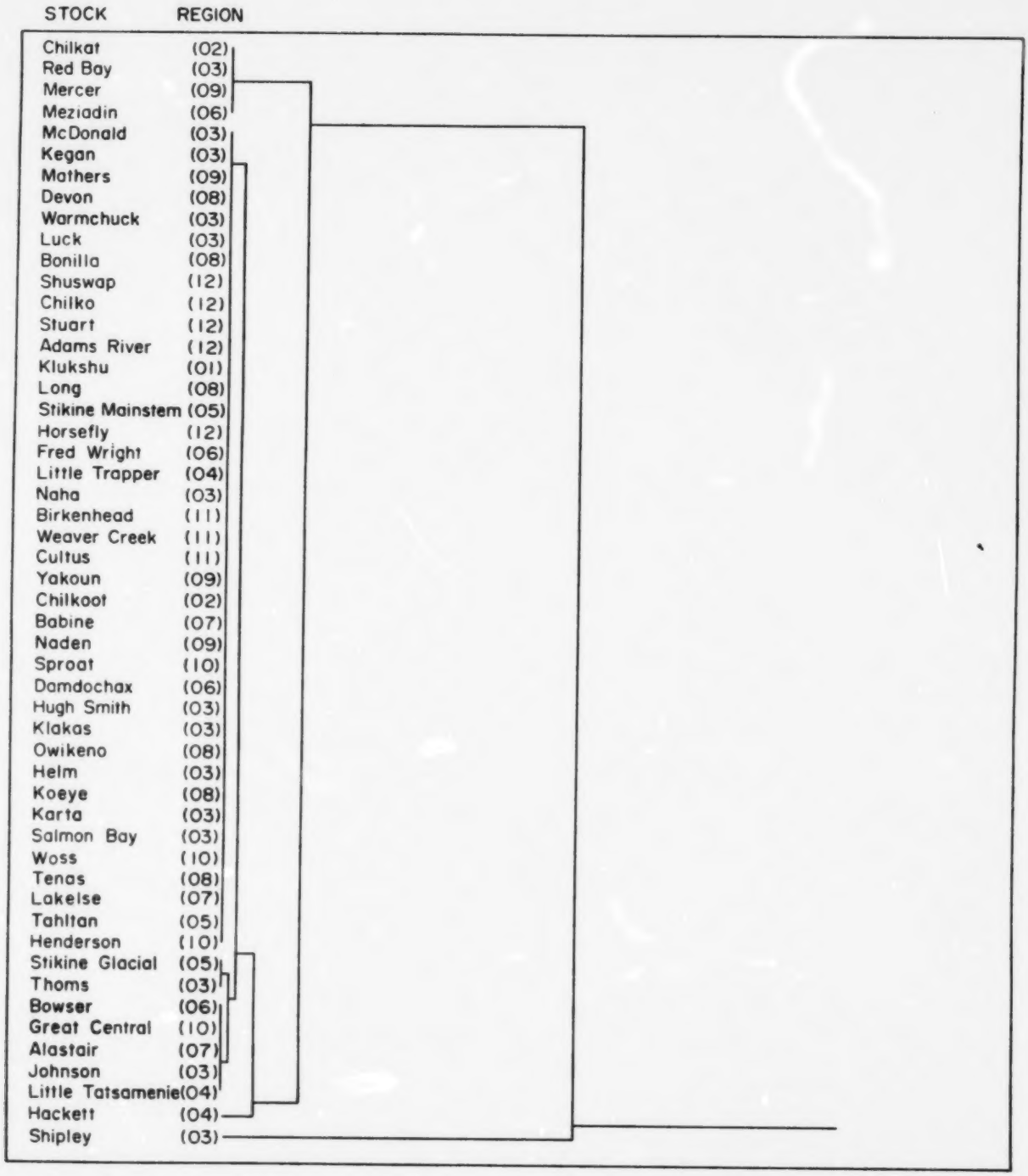

Fig. 4. Similarity dendrogram for 52 sockeye populations based on freshwater age composition only. Samples range in size from 49 to 3010 and were collected between 1979 and 1986.

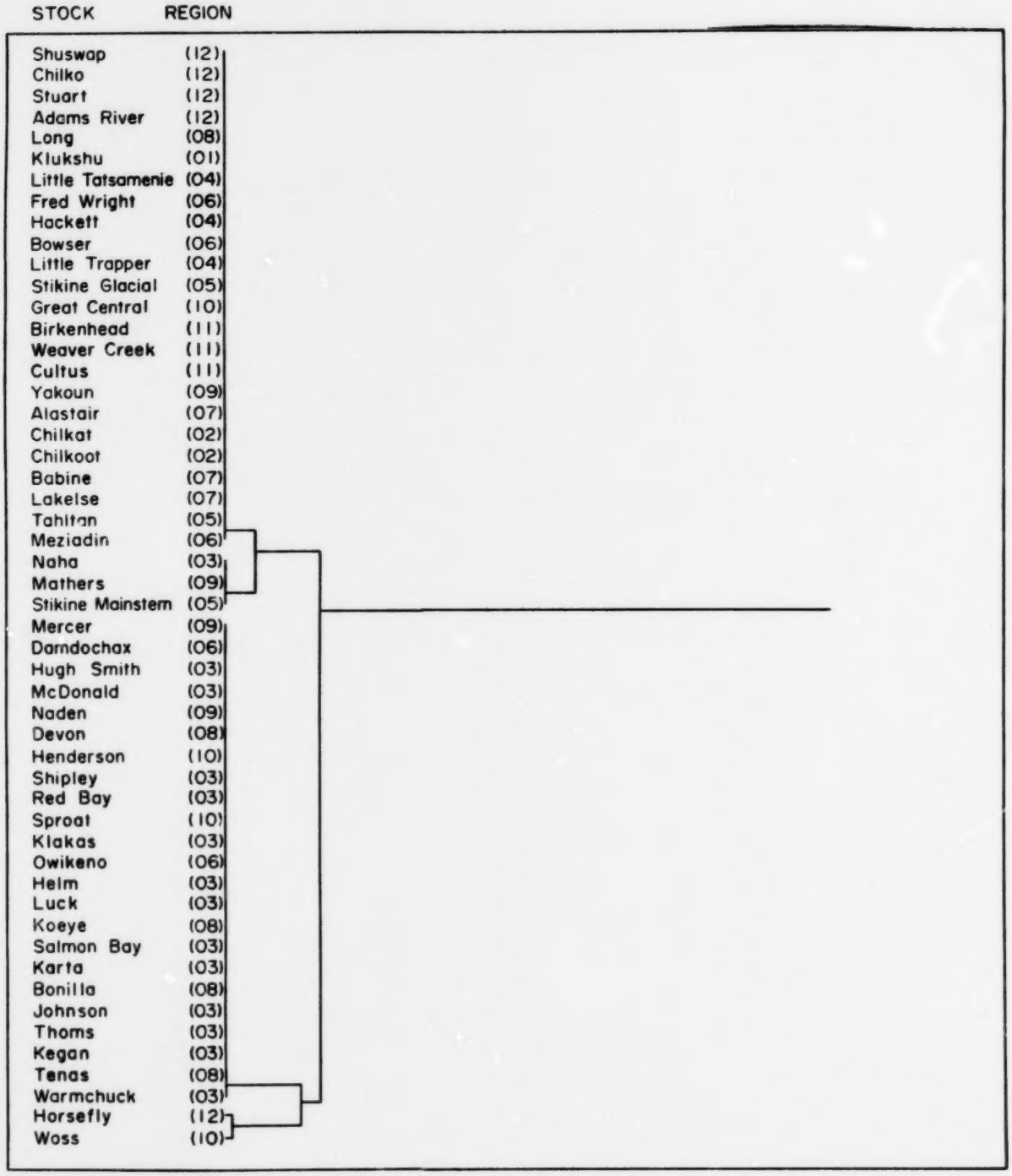

Fig. 5. Similarity dendrogram for 52 sockeye populations based on brain parasite (Myxobolus neurobius) prevalence only. Samples range in size from 21 to 1039 and were collected between 1982 and 1985.

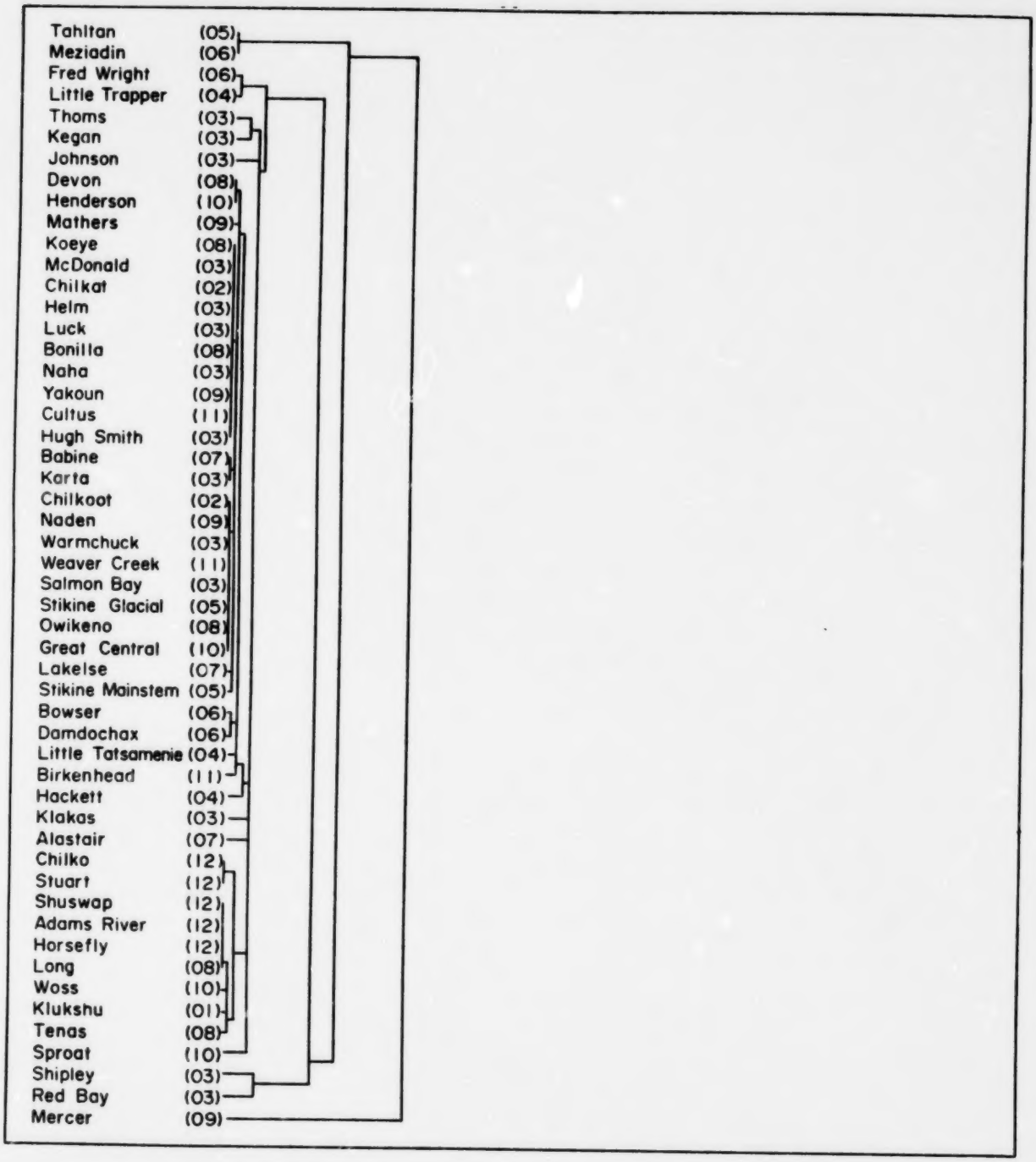

Fig. 6. Similarity dendrogram for 52 sockeye populations based on electrophoretic differences in five polymorphic enzymes (Pgm-1, Pgm-2, Ldh-4, Idh-3 and Idh-4). Samples range in size from 26 to 710 and were collected between 1982 and 1985.

Appendix Table 1. Summary of scale samples collected routinely from sockeye spawning escapements in southern Southeast Alaska and Canada, 1982-1986. This table does not include matched electrophoretic-parasite-scale samples (see Appendix table 3).

State/ Province	Statistical Area	System	Year				
			1982	1983	1984	1985	1986
Alaska	101-11	Filmore L.	143	146			
		Hugh Smith L.	3,009	1,107	1,591	1,170	2,172
	101-45	Leask L.	257	58		35	370
	101-80	McDonald L.	629	1,366	927	537	610
	101-90	Naha L.	184	1,648	500	405	1,001
		Helm L.	276	274	29	367	350
	102-20	Paul L.	106		123		
	102-30	Johnson L.	337	563	240	358	14
		Kegan L.	1,776	1,699	321	444	240
	102-60	Karta L.	1,429	921	224	1851	595
	103-15	Klakas L.	356	691	180	318	
	103-25	Hetta L.	745	114	199	436	500
	103-60	Klawock L.	725	100	191		700
	103-80	Warm Chuck L.	332	1,755	572	686	414
	103-90	Sarkar L.	538	140	316	457	416
	105-31	Kushneahin L.	30	29	50	100	104
	105-42	Sutter L.	177		69		65
	105-43	Shipley L.	92		105		
	106-10	Trumpeter L.	120	452	75	480	276
		Luck L.	365	445	335	265	488
	106-30	Sweetwater L.	346				276
	106-41	Salmon Bay L.	1,302	527	592	1,342	1528
		Red Bay L.	316	367	271	520	608
	106-42	Kah Sheets L.	25	194	161		26
	106-44	Petersburg L.	31	242	474	237	551
	107-30	Thoms L.	508	419	607	337	530
	109-20	Falls L.	532	727	688	879	
	109-52	Kutlaku L.	345		492	413	525
	109-62	Alecks L.	396				520
	111-32	Crescent L.	611	1648	1140	1303	
	111-50	Speel L.	312	793	765	396	
British Columbia	01	Naden L.	50	26			
		Yakoun L.		100			
	03	Bowser L.	20	65		164	100
		Damdochax L.	85	173	50	100	100
		Fred Wright L	23	295	50	100	100
		Meziadin L.	1075	1200	1200	1200	1000

Appendix Table 1 (cont'd)

State/ Province	Statistical Area	System	Year				
			1982	1983	1984	1985	1986
British Columbia	10	Long L.	65			135	
	12	Nimpkish L.			44	80	
	21	Cheewhat L.				191	272
	22	Hobiton L.	996	1092	1112	736	138
	23	G. Central L.	800	800	800	400	400
	24	Muriel L.			91	13	130
		Henderson L.	200	200	200	5	100
		Sproat L.	1000	1000	1000	450	400
	29	Adams R.	350	253	120	368	872
		Birkenhead R.	720	585	328	596	736
		Chilko L.	595	209	498	588	1162
		Cultus L.	130	120	262	84	65
		Horsefly R.	240	134	202	473	360
		Sushwap R.	360	221	4	62	230
		Stellako R.	136	258	247	273	50
		Weaver Ck.	480	710	168	570	779
		Stuart L.	458	450	1900	1064	1175
Transboundary Systems	Stikine	Stikine R. (mainstem)		100		490	66
		Christina L.			68	130	168
		Chutine R.			54	90	109
		Iskut R.		24	125	159	
		Scud R.			40	68	
		Tahltan L.	1460	2125	2197	2641	760
	Taku	Hackett R.				278	250
		Kuthai L.	219		242		
		L. Tatsamenie L.		255	183	1000	750
		L. Trapper L.	611	1939	1300	1358	850
	Alsek	Klukshu R.	523	1565	400	1700	1006

Appendix Table 2. Summary of brain parasite samples collected from sockeye salmon spawning escapements in southern Southeast Alaska and Canada, 1982-1986.

State/ Province	Statistical Area	System	Year				
			1982	1983	1984	1985	1986
Alaska	101-11	Hugh Smith L.	30	75			
	101-45	Leask L.					41
	101-80	McDonald L.	30	100			50
	101-90	Naha L.		57	50		50
		Helm L.		50			51
	102-30	Johnson L.		50			
		Kegan L.	30	50			50
	102-60	Karta L.	30	50			10
	103-15	Klakas L.		50			
	103-80	Warm Chuck L.		50			
	103-90	Sarkar L.					44
	105-42	Sutter L.					36
	105-43	Shipley L.		49			
	106-10	Luck L.		50			21
	106-41	Salmon Bay L.	30	45			51
		Red Bay L.		70			52
	106-44	Petersburg L.					50
	107-30	Thoms L.		50			50
	111	Speel L.		50			
	111	Crescent L.		50			
British Columbia	01	Naden R.	50	26			
		Yakoun L.	50				
	02	Mercer L.	50	100			
		Mathers L.	50				
	03	Bowser L.		64	87		183
		Damdochax L.		100	100		100
		Fred Wright L.		100	100		190
		Meziadin L.	100	100	100		294
	04	Alastair L.	100	100			
		Babine L. (early)			100	158	
		Fulton R.	100	100		300	
		Four Mile R.	71				
		Pinkut R.	100	151		200	
		Lakelse L.	48	100			
	05	Banks L.					100
		Bonilla L.		100			
		Devon L.				100	
		Lowe L.					93
		Mikado L.					100
	06	Canoona R.					100
	07	Kitlope L.					50
		Tankeeah L.					100

Appendix Table 2 (cont'd)

State/ Province	Statistical Area	System	Year				
			1982	1983	1984	1985	1986
British Columbia	08	Kimsquit L.					100
		Koeye L.				100	
		Tenas L.				100	
	09	Owikeno L.	100		100		
	10	Long L.	84		154		
	12	Woss L.				100	
	23	Cheewhat L.		100			
		G. Central L.		143			
		Henderson L.		154			
		Sproat L.		183			
	24	Kennedy L.					91
	29	Adams R.	100	100			
		Birkenhead R.	72				100
		Chilko L.		100			
		Cultus L.				100	
		Horsefly R.				100	100
		Shuswap R.	100				100
		Takla L.	100				100
		Stellako R.	100				100
		Weaver Ck.	100				100
		Anderson L.					200
		Seymour R.					100
		Fraser L.					100
		Pitt L.					100
		Harrison L.					100
Transboundary Systems	Stikine	Stikine R. (mainstem)	105	118			106
		Christina L.			76		
		Chutine L.			100	50	64
		Chutine R.			62	50	50
		Iskut R.		110	151	159	150
		Scud R.			50	68	
		Tahltan L.	100	102		100	
	Taku	Taku R. (mainstem)					466
		Nakina R. (mainstem)					53
		Hackett R.				63	
		Kuthai L.					74
		L. Tatsamenie L.				100	
	Alsek	L. Trapper L.	103	100			
		Klukshu R.		94			

Appendix Table 3. Summary of matched electrophoretic - brain parasite - scale samples collected from spawning escapements in southern Southeast Alaska and Canada, 1982-1986.

State/ Province	Statistical Area	System	Year				
			1982	1983	1984	1985	1986
Alaska	101-11	Hugh Smith L.	50	96			
	101-45	Leask L.					41
	101-80	McDonald L.	50	100			50
	101-90	Naha L.		100	50		50
		Helm L.		50			51
	102-30	Johnson L.		80			
		Kegan L.	100	100			50
	102-60	Karta L.	50	100			10
	103-15	Klakas L.		100			
	103-80	Warm Chuck L.		100			
	103-90	Sarkar L.					44
	105-42	Sutter L.					36
	105-43	Shipley L.		50			
	106-10	Luck L.		50			21
	106-41	Salmon Bay L.	69	75			51
		Red Bay L.		70			52
	106-44	Petersburg L.					50
	107-30	Thoms L.		75			50
	111	Speel L.		50			
	111	Crescent L.		50			
British Columbia	01	Naden R.	50	26			
		Yakoun L.	50				
	02	Mercer L.	50	100			
		Mathers L.	50				
	03	Bowser L.		64	87		183
		Damdochax L.		100	100		100
		Fred Wright L.		100	100		190
		Meziadin L.	100	100	100		294
	04	Alastair L.	100	100			
		Babine L. (early)			100	158	
		Fulton R.	100	100		300	
		Four Mile R.	71				
		Pinkut R.	100	151		200	
		Lakelse L.	48	100			
	05	Banks L.					100
		Bonilla L.		100			
		Devon L.				100	
		Lowe L.					93
		Mikado L.					100
	06	Canoona R.					100

Appendix Table 3 (cont'd)

State/ Province	Statistical Area	System	Year				
			1982	1983	1984	1985	1986
	07	Kitlope L.					50
		Tankeeah L.					100
	08	Kimsquit L.					100
		Koeye L.				100	
		Tenas L.				100	
	09	Owikeno L.	100		100		
	10	Long L.	84		154		
	12	Woss L.				100	
	23	Cheewhat L.			100		
		G. Central L.		143			
		Henderson L.		154			
		Sproat L.		183			
	24	Kennedy L.					91
	29	Adams R.	100	100			
		Birkenhead R.	72				100
		Chilko L.		100			
		Cultus L.				100	
		Horsefly R.				100	100
		Shuswap R.	100				100
		Takla L.	100				100
		Stellako R.	100				100
		Weaver Ck.	100				100
		Anderson L.					200
		Seymour R.					100
		Fraser L.					100
		Pitt L.					100
		Harrison L.					100
Transboundary Systems	Stikine	Stikine R. (mainstem)	105	118			106
		Christina L.			76		
		Chutine L.			100	50	64
		Chutine R.			62	50	50
		Iskut R.		110	151	159	150
		Scud R.			50	68	
		Tahltan L.	100	102		100	
	Taku	Taku R. (mainstem)					466
		Nakina R. (mainstem)					53
		Hackett R.				63	
		Kuthai L.					74
		L. Tatsamenie L.				100	
		L. Trapper L.	103	100			
	Alsek	Klukshu R.		94			